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Studies on Fossil Phyllodont Fishes: *Casierius*, a New Genus of Albulid from the Cretaceous of Europe and North America

by RICHARD ESTES¹⁾

The first paper in this series (ESTES, 1969) described tooth plates of *Phyllodus*, *Egertonia*, *Paralbula*, *Pseudoegertonia*, and *Eodiaphyodus*. These genera were referred to an extinct family of elopiform, albuloid fishes, the Phyllodontidae, based entirely on tooth plates. Teeth of all these genera are phyllodont, the replacement teeth arranged in either alternating or directly successional stacks. This phyllodont tooth adaptation may also occur in other teleost families, including the labroids Labridae, Odacidae, and Scaridae, as well as in Sciaenidae, Carangidae, and Diodontidae. Such an adaptation seems to have been associated primarily with near-shore or reef fishes subsisting on a diet of hard-shelled invertebrates.

Described Cretaceous specimens from Italy and France, and new material from England and Texas, indicated that at least one phyllodont genus may be referable to the Albulidae, making a total of eight families in which this adaptation is known to occur.

Family Albulidae

Casierius, n. gen.

Type species: *Glossodus heckelii* COSTA 1864, p. 109, Tav. 9, Fig. 12; *non Glossodus* AGASSIZ 1828 (in Spix, Piscium Brazil.), *non Glossodus* M'COY 1848, Ann. Mag. Nat. Hist. 2, p. 127, *non Glossodus* COSTA 1851, N. Jahrb., p. 184.

Etymology: Named for Professor EDGARD CASIER, Institut Royal des Sciences Naturelles, Brussels, for his contributions to the study of fossil fishes.

Diagnosis: Albulid fishes known only from pterygoid, parasphenoid and basi-branchial tooth plates. In contrast to known albulids: teeth phyllodont, flattened; replacement alternating; tooth crowns smooth or with a fine sculpture; pulp cavity very small. Basibranchial and parasphenoid tooth plates about twice as long as wide, similar in shape to those of Recent *Albula*; pterygoid plate about equal in length to basibranchial plate, and relatively wider than that of *Albula*.

Age and Distribution: Albian (Italy, France, England, United States).

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Casierius heckelii (COSTA)

Type specimen: Istituto di Paleontologia dell' Università di Napoli, No. Inv. F1.

Comments: This species was described by COSTA (1864, Tav. 9, fig. 12–13) based on two specimens from Cretaceous limestones at Pietraroia, Italy. The type specimen is refigured here (Plate 1, Fig. 1a); the referred specimen is now lost, but probably is not referable to *C. heckelii* because of its columnar rather than flattened teeth. The type specimen is flattened by crushing and about three layers of phyllodont teeth are present. The latter are smooth or finely-sculptured and are 0.8–1.7 mm in diameter. The main part of the specimen is probably a parasphenoid tooth plate, because of the presence of a bony shelf at the posterior end (Plate 1 Fig. 1a). Irregular remnants of the opposing basibranchial tooth plate still adhere to it, and the flattened, open root cavities of the teeth are well shown. The presumed parasphenoid tooth patch is 36.0 mm long and 19.4 mm wide.

CORNUEL (1877) referred a tooth plate from the early Cretaceous (Albian) Gault clay in France to *Egertonia*, as a new species *E. gaultina* (Museum National d'Histoire Naturelle, Paris, no. 1885–19, Moutier-en-der, Haute-Marne). The presence, in the phyllodontid *Egertonia*, of a greater number of tooth layers, different tooth plate proportions, and thick, glossy teeth with a well-defined central cavity, preclude the CORNUEL specimen from inclusion in that genus (ESTES, 1969). New Albian material from England and Texas described below, when compared with the COSTA and CORNUEL specimens, shows that the latter is probably the anterior half of a basibranchial tooth plate (CORNUEL, 1877, Pl. 11, figs. 31, 32; Plate 1, Fig. 2, this paper). Although the Albian material is about twice the size of the type specimen of *C. heckelii*, no morphological differences occur between them, and CORNUEL's species *gaultina* is here considered part of the synonymy of *Casierius heckelii*.

The following specimens are also referred to *Casierius heckelii*: British Museum (Natural History) 47207, basibranchial tooth plate, and P. 50594, right pterygoid tooth plate, from the Gault clay, Folkestone, Kent, England (Plate 1, Fig. 3). Field Museum of Natural History PF 5739, right pterygoid tooth plate, and PF 5740, fragments of tooth plates from the Trinity sands, Greenwood Canyon, off Braden Branch of Denton Creek, 2.5 miles SW of Forestburg, Montague County, Texas, USA (Plate 2).

Description of referred specimens: BMNH 47207, a basibranchial tooth plate, is an elongated mass of superimposed teeth lacking indication of attachment bone. The plate is 9 mm deep, 52 mm long and 26 mm wide as preserved. In lateral view, the plate is thickened and convex, its presumed posterior end tapering and becoming flattened as in *Albula*. Individual teeth range from 1.0–3.5 mm in diameter; most of them are rounded or slightly irregular in outline and are flattened hemispheres in cross-section. The majority of teeth have their crowns worn away by trituration, but unworn crowns are smooth or have a fine sculpture. There are three or four layers of superimposed teeth over most of the tooth plate, and individual teeth alternate with one another in arrangement. The teeth are composed of orthodentine with a well-defined outer layer of vitrodentine or durodentine (Plate 1, Fig. 3d). Bases of the teeth are flattened, occasionally with a weak lateral rim, and only a very small central cavity is present.

BMNH P. 50594, a right pterygoid tooth plate, is elongated and asymmetrical with a concave triturating surface. Tooth size is as in the basibranchial plate; the plate is 62 mm long and 27 mm wide as preserved. The presumed anterior end is pointed, and the presumed posterior end more bluntly rounded. As in the basibranchial plate there are three or four superimposed layers of teeth. The most basal (dorsal) layers of teeth are imbedded in a mass of attachment bone formed of parallel trabeculae perpendicular to the occlusal surface (Plate 1, Fig. 3d).

The Texas specimens are similar to the English ones in tooth shape, implantation, and weak sculpture. FMNH PF 5739, a right pterygoid tooth plate, is similar in shape to the English specimen, but is not as complete anteriorly. Tooth diameter ranges from 1.0–2.3 mm, and the plate is 40 mm long and 23 mm wide as preserved. The fragments of tooth plates (FMNH PF 5740) have teeth from 1.5–3.0 mm in diameter.

Discussion: The tooth characteristics described for the referred specimens can all be seen in the type specimen (Pl. 1, Fig. 1a) or in the CORNUEL specimen (Pl. 1, Fig. 2a–b), except that tooth crown sculpture in the latter is more pronounced than in the others. The British Museum specimens were mentioned by WOODWARD (1901, p. 73) and tentatively referred to the Albulidae. He noted the resemblance of these specimens to those of «*Glossodus*» *heckelii* and «*Egertonia*» *gaultina* that is confirmed here. He also noted a resemblance to *Albula* («*Pisodus*») *foucardi*, but the latter is not phyllodont.

One of the characters used to define the Phyllodontidae is the presumed absence of pterygoid tooth plates (ESTES, 1969). Although many finds referable to the latter family have been described, only basibranchial and parasphenoid tooth plates have been identified so far. Both English and American localities have produced pterygoid tooth plates referable to *Casierius*, plates that are of the same general form as in Recent *Albula*. The basibranchial tooth plate of *Casierius* is about twice as long as wide, as in *Albula*, rather than about 1.5 times as long as in the phyllodontids. If my orientation of the basibranchial tooth plate of *Casierius* is correct, then (as in *Albula*) the anterior part is convex and bears relatively large teeth, while the posterior part is flattened and has relatively smaller teeth (cf. Pl. 1, Figs. 1b and 3a). In phyllodontids, the bone articulation surfaces on the basibranchial tooth plates indicate that the convex portion is posterior, in contrast to albulids (ESTES, 1969, fig. 2b–e). Unfortunately, the absence of skull and branchial bone articulation surfaces on the tooth plates of *Casierius* makes determination of orientation difficult. Large parasphenoid-basibranchial tooth plates occur frequently in Recent elopomorph and osteoglossomorph teleosts but not in higher forms; those of the albuloids, especially *Albula*, are much better developed (NELSON, 1968, 1969). Although the teeth of *Casierius* are phyllodont, as in Phyllodontidae, the wide distribution of this character noted at the beginning of this paper suggests that phyllodonty should not supersede the other characters in classification. For the above reasons *Casierius* is here referred to the Albulidae, although classification based on shape and position of tooth plates without knowledge of the remainder of the skeleton must be tentative and may be artificial.

Geological setting and faunal associates of *Casierius*: The ichthyofauna from Pietraroia includes the following forms, according to ARAMBOURG (1952):

«Holostei»

<i>Lepidotes</i>	<i>Sauropsidium</i>
<i>Ionoscopus</i>	<i>Elopopsis</i>
<i>Coelodus</i>	<i>Hemielopopsis</i>
<i>Palaeobalistum</i>	<i>Hypsospondylus</i>
<i>Notagodus</i>	<i>Chanos</i>
<i>Propterus</i>	<i>Chirocentrites</i>
Teleostei	<i>Diplomystus</i>
<i>Anaethalion</i>	
<i>Clupavus</i>	

The mixture of Jurassic and Cretaceous species of these genera indicated to Arambourg that the fauna from Pietraroia was of «Albo-Aptian» age. The other known specimens of *Casierius* are Albian (probably early Albian), and it is therefore possible that the limestones at Pietraroia may also be of early Albian age.

The Gault Clay is widespread in the Anglo-Franco-Belgian Basin. It is composed mainly of thick blue clays that contain a rich ammonite fauna of Albian age, and it is the result of widespread marine transgression on the continental Wealden beds (GIGNOUX, 1955).

Dr. COLIN PATTERSON has kindly provided me with a faunal list for the English Gault; it includes the following genera:

Selachii	Chimaeroidei	Teleostei
<i>Acrodus</i>	<i>Ischyodus</i>	<i>Thrissopater</i>
<i>Synechodus</i>	<i>Edaphodon</i>	<i>Plethodus</i>
<i>Heterodontus</i>	<i>Elasmodectes</i>	<i>Osmeroides</i>
<i>Hybodus</i>	Coelacanthini	<i>Syllaemus</i>
<i>Notidanus</i>	<i>Macropoma</i>	<i>Xiphactinus</i>
<i>Scapanorhynchus</i>	«Holostei»	? <i>Enchodus</i>
<i>Lamna</i>	<i>Protosphyraena</i>	? <i>Ichthyotringa</i>
<i>Isurus</i>	<i>Lepidotes</i>	<i>Apateodus</i>
<i>Squatina</i>	<i>Coelodus</i>	<i>clupeomorph</i>
<i>Squalus</i>		

The fauna is of marine type, and is most closely related to that of the Chalk. None of the known Gault teleosts are likely to have had teeth of *Casierius* type, although the number of identifiable teleost specimens is small (C. PATTERSON, in litt., 1969).

The Trinity sands contain both marine and freshwater deposits, and reflect marine transgression with a fluctuating shoreline. The localities yielding *Casierius* in Texas have produced an undescribed fauna primarily of freshwater type, although some brackish or anadromous forms may be included. Teeth of small sharks of *Acrodus* type, teeth and scales of *Lepidotes*, abundant scales representing four or five different caturids, lungfish teeth (cf. *Ceratodus*), and bones of several different families of frogs are common. Remains of lizards, non-marine turtles, crocodiles, and both carnosaurian and ornithopod dinosaurs occur as well (PATTERSON, 1956). The hybodont shark *Lonchidion* (ESTES, 1964; PATTERSON, 1966) is also present, as well as the salamander *Prosiren* (GOIN and AUFFENBERG, 1958; ESTES, 1969a).

The presence of well-preserved specimens of *Casierius* in both freshwater and marine deposits is interesting, for *Albula* today is not diadromous. Mr. JOHN THURMOND, who is describing the fossil fishes of the Trinity deposits, states (in litt., 1969) that he has found *Casierius* specimens in one of his brackish-water localities.

Relationships of *Casierius* outside the Albulidae: The phyllodont teeth of *Casierius* suggest a possible link between Albulidae and Phyllodontidae. An albulid such as *Casierius*, if it lost or strongly reduced the pterygoid tooth plates, would be a suitable ancestor for the phyllodontids. *Casierius* does not show such a tendency to reduction, but its Albian age is early enough so that reduction would be possible by Campanian time, when the first phyllodontids appear (ESTES, 1969). However, as noted above, the few characters available and the parallel development of phyllodont teeth in a number of other teleost families makes classification of these isolated tooth plates somewhat artificial, without knowledge of more complete specimens.

Acknowledgements

I am grateful to Dr. RAFFAELE SCORZIELLO for loaning me the type specimen of *Casierius heckelii*, to Dr. COLIN PATTERSON for helpful comments and for providing the English Gault Clay specimens and faunal list, to Dr. ROBERT DENISON for providing the Trinity specimens, and to Dr. CÉCILE POPLIN for sending photographs of the CORNUEL specimen (now in the Museum National d'Histoire Naturelle, Paris). Mr. FREDERICK MAYNARD (Boston University) took the other photographs. This research was supported in part by National Science Foundation Grant GB-7176.

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Plate I

- Fig. 1a. *Casierius heckelii*, n. gen., type specimen, Instituto di Paleontologia, Università di Napoli, No. Inv. F1. Parasphenoid tooth plate overlain by portion of basibranchial tooth plate (outlined by dotted line).
- Fig. 1b–c. *Albula*, Recent. b, basibranchial tooth plate of *A. vulpes*, United States National Museum Fish Osteological Collection; c, left pterygoid tooth plate of *A. vulpes*, Museum of Comparative Zoology Fish Osteological Collection, Harvard University; anterior to the right.
- Fig. 2a–b. *Casierius heckelii*, n. gen., Gault Clay, Moutier-en-der (Haute-Marne) France. a, occlusal, and b, basal views of fragmentary basibranchial plate, Museum National d'Histoire Naturelle 1885–19; anterior to the left?
- Fig. 3a–d. *Casierius heckelii*, n. gen., Gault Clay, Folkestone, Kent, England. a, occlusal, and b, lateral views of basibranchial plate, anterior to the left?, British Museum (Natural History) 47207; c, occlusal view of right pterygoid tooth plate, BMNH P. 50594, anterior to the top, bracket indicates site of cross-section; d, much enlarged cross-section of BMNH P. 50594 at anterior end, showing phylloidont replacement pattern, pulp cavity and dentine layers of teeth, and trabecular attachment bone at the base of the plate.

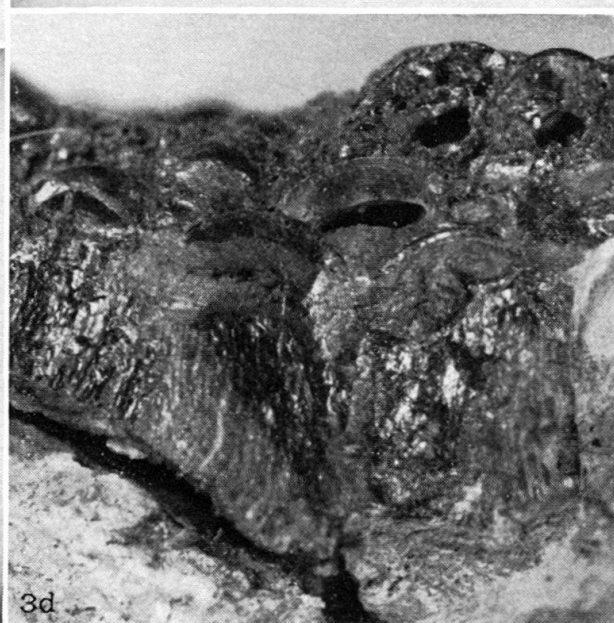
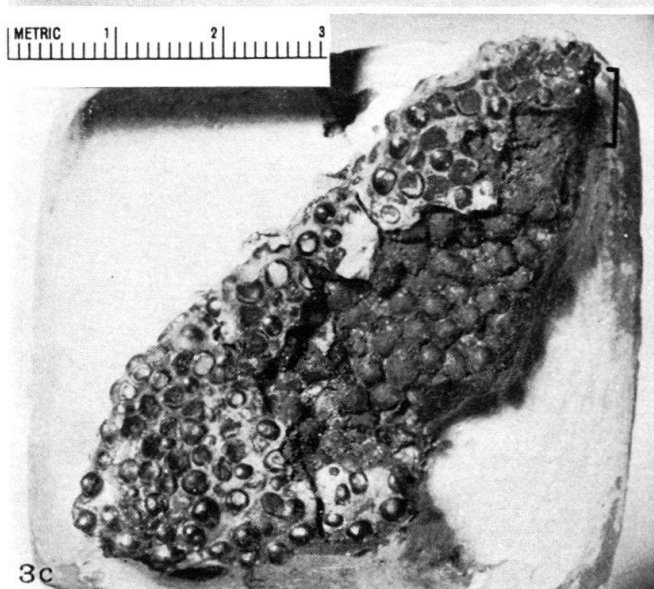
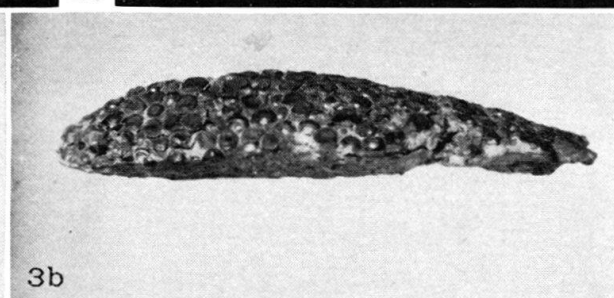
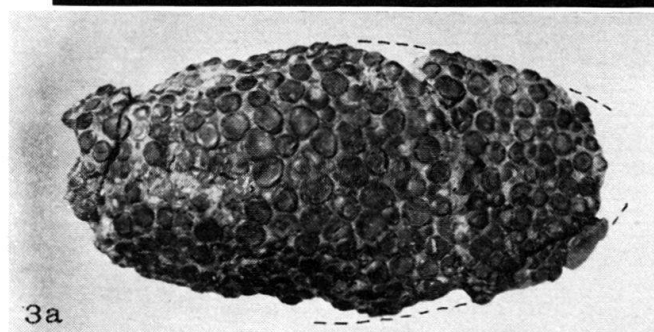
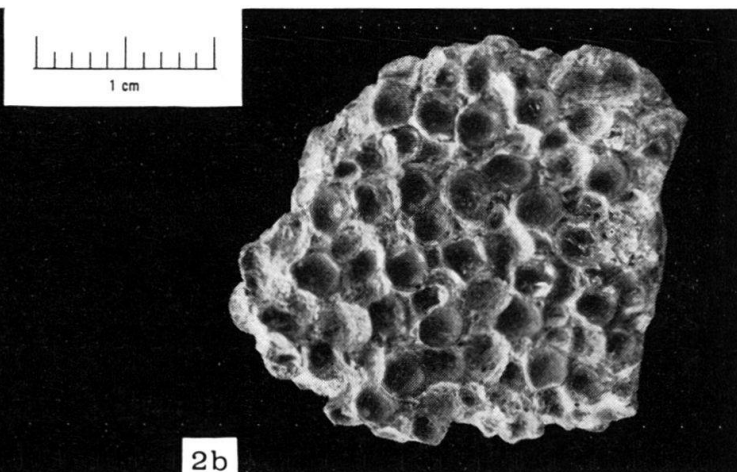
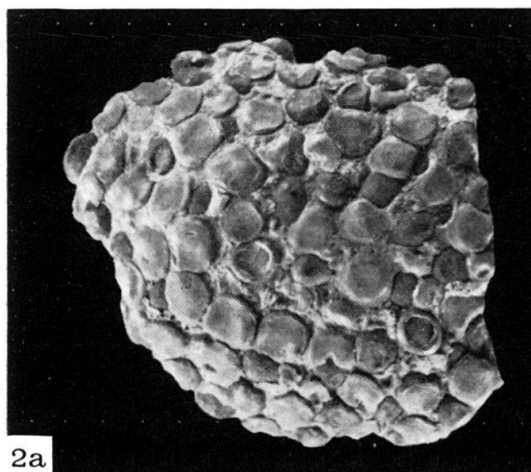
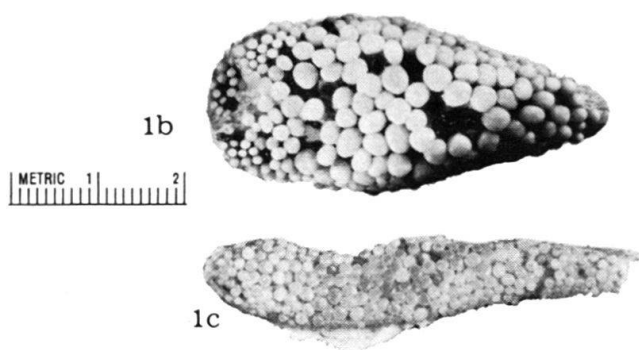
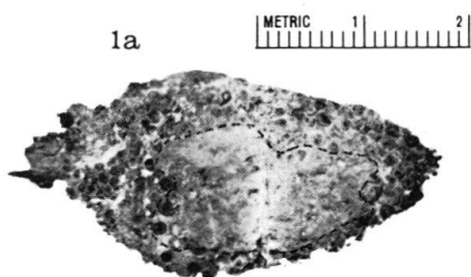


Plate II

Fig. 1a–c. *Casierius heckelii*, n. gen., Trinity sands, Texas, U.S.A.; a, occlusal, b, medial, and c, basal views of Field Museum of Natural History PF 5739, fragmentary right pterygoid tooth plate; anterior to the right, all X3.

